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THE SYSTEMATIC POSITION OF THE FAMILY IRONIDAE AND ITS RELATION TO THE DORYLAIMIDA

by

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ABSTRACT

A critical review is made of the similarities and differences existing between the Ironidae and the Dorylaimida. The most important diagnostic features of the main groups of Dorylaimida, up to the superfamily level, and of the Enoplidae are listed. The family Ironidae is subdivided into two subfamilies of which the Coniliinae constitute a new subfamily with *Conilia* Gerlach, 1956 as the type genus.

From the detailed comparison of both groups it is concluded that the differences are important and that the similarities are probably the result of parallel evolution, occurring in two branches that evolved independently from a remote enoplid ancestor.

It is further argued that Ironidae do not fit well in Tripyloidea and are at present better included in Enoploidea.

On several occasions the similarities between *Ironidae* and *Dorylaimida* have been stressed, the extreme being the inclusion of the genera of the *Ironidae* in the family *Dorylaimidae* (Wieser, 1953). *Ironidae* are now usually classified under *Tripyloidea* in the *Enoplida*, but a close relationship between *Ironidae* and *Dorylaimida* has been postulated, with *Ironidae* representing the ancestral type.

COMPARISON OF THE MAIN FEATURES OF IRONIDAE AND DORYLAIMIDA

Differences can be observed in e.g. the number and position of the lips (except *Ironella*), structure and outlet of the excretory system, position of the oesophageal gland outlets and habitat of most representatives.

Similarities exist in general body shape, position and shape of the amphideal fovea, structure of the feeding apparatus, structure of the female reproductive system and of the male copulatory apparatus. It is clear that the *Dorylaimida*, having ordinal rank, are more heterogenous than the *Ironidae*, even though they may represent a superfamily. Therefore it is necessary to mention briefly the main characters of the subdivisions that have to be compared (Classification according to Coomans and Loof, 1970).

Suborder *Mononchina* : oesophagostome (1) (commonly called stoma or buccal cavity) barrel-shaped with heavily sclerotized walls, with 1-3 large teeth. If only one large tooth is present it is the dorsal one. Anterior somatic muscles controlling

(1) Modification of the term oesophastome used by Inglis (1966) and Coomans (1975).

protrusion and retraction of oesophagostome, hence no real protractor muscles of the oesophagostome differentiated. Oesophagus cylindrical, with the dorsal gland nucleus (DN) far behind the outlet (DO) but anterior to the outlets of the first pair of ventrosublateral glands (S_1O). Excretory system usually obscure, but where observed consisting of two uninucleate long-necked renette cells connected to an ampulla and opening through an excretory pore situated behind the nerve ring. Caudal glands present or absent.

Suborder *Bathyodontina* : oesophagostome consisting of a wider anterior and narrower posterior portion, with weakly to strongly sclerotized walls and only one tooth of varying size but ventrosublateral in position. Protractor muscles of the oesophagostome differentiated, posteriorly attached to the oesophageal wall. Oesophagus cylindrical, with DN far behind DO, at the level of or behind S_1O. Excretory system obscure, pore situated behind nerve ring. Caudal glands present. This suborder comprises two superfamilies which show some important differences : (1) *Bathyodontoidea* have a narrow elongated oesophagostome, with a very small tooth and weakly sclerotized walls ; the second pair of ventrosublateral nuclei S_2N lies far behind the outlets (S_2O) ; cardiac glands lacking. (2) *Mononchuloidea* have a wide anterior oesophagostome with a large, grooved tooth and well sclerotized walls, S_2N lie opposite S_2O ; cardiac glands present.

Suborder *Dorylaimina* : oesophagostome with a long and narrow tooth or odontostyle of ventrosublateral origin, and weakly sclerotized walls. Well developed protractor muscles posteriorly attached to the oesophageal wall. Oesophagus consisting of a narrow anterior part and a wider posterior one. DN a short distance behind DO, well anterior to S_1O ; S_1N opposite S_1O. Excretory system and pore obscure. Caudal glands absent. Although several superfamilies have been proposed, only two are accepted : (1) *Nygolaimoidea* with ventrosublateral tooth and free cardiac glands ; both S_1N at about the same level and equally developed. (2) *Dorylaimoidea* with an axial odontostyle and usually no free cardiac glands ; S_1N usually at different levels and S_1N_1 often smaller than S_1N_2.

Two more suborders (*Diphtherophorina* and *Trichosyringina*) show a number of specialised and aberrant characters that obscure their origin. This is especially so for the *Diphtherophorina*. The *Trichosyringina* can be related to the *Dorylaimina* on the basis of their juvenile stages. Both groups however are not essential for the discussion below since they are by no means primitive dorylaims.

Family *Enoplidae* : oesophagostome consisting of two parts : (1) a double walled anterior part with three single, two single ventrosublateral and one double dorsal or a single dorsal and two double ventrosublateral teeth ; (2) an elongated odontophore region. Protractor muscles controlling protrusion of oesophagostome intra-oesophageal ; 4 retractor muscles outside oesophagus. Oesophagus cylindrical with 5 glands, the nuclei of which occur at the basis of the oesophagus ; outlets only known for the anterior three glands : S_1O anterior to DO. Excretory system consisting of a well developed, single renette cell, opening medio-ventrally between the first and second circlet of cephalic sense organs. Caudal glands usually present.

The family can be subdivided into two subfamilies : (1) *Ironinae* with anteriorly attenuating body ; relatively narrow mouth opening ; usually flattened spicules, usually with median sclerotization and ventral flange ; gubernaculum with sclerotized proximal and lateral margins of the corpus ; and (2) *Coniliinae* n. subf. : Ironidae. Body cylindrical. Mouth opening wide ; cheilostome forming a wide cylinder. Spicules long and tubiform. Type genus : *Conilia* Gerlach, 1956 ; other genus : *Ironella* Cobb, 1920.

In Ironidae as well as *Dorylaimida* the anterior part of the feeding apparatus (modified anterior feeding apparatus or oesophagostome) shows a marked tendency to become elongated. In *Ironidae* typically three teeth are present, although the dorsal one is often and both ventrosublateral ones are rarely (*Ironella*) double. Within the *Dorylaimida* three teeth only occur in the *Mononchina*, while the other forms possess one tooth ; even in *Mononchina* there is a tendency towards a reduction of the two ventrosublateral teeth.

So we see that the occurrence of three teeth in the *Dorylaimida* is rather exceptional and, if so, the oesophagostome is not elongated. In those cases where the oesophagostome is elongated its lining provides a long supporting structure (odontophore) and is partly double walled enabling a forward movement of the whole system, so that teeth or tooth can protrude from the mouth for seizing or puncturing the prey. In *Ironidae* protraction of the oesophagostome is mediated by three protractors confined within the oesophageal wall (one per sector), while the inclination of the teeth is operated by separate muscles also inside the oesophageal wall (cf. VAN DER HEIDEN, 1975). In *Dorylaimida* this protraction typically is controlled by eight protractor muscles lying outside the oesophageal wall, but usually posteriorly attached to it. The retraction system is similar in both groups in that the retractor muscles are outside the oesophageal wall, attach to it anteriorly and to the body wall posteriorly. However, the number and position of retractor muscles are different : typically four (two subventral and two laterodorsal) in *Ironidae*, typically eight submedian ones in *Dorylaimida*.

In both groups the teeth (or tooth) are (is) replaced during moulting by replacement teeth (tooth) formed during the previous moulting and stored behind the functional teeth (tooth). *Ironidae* - juveniles have their replacement teeth about one lip-region width (or even more) behind the functional ones. That is compared to teeth-size rather far behind, compared to oesophagostomal length rather anterior. In *Mononchina* the replacement teeth are stored partly inside the functional ones ; in *Bathyodontina* the replacement tooth occurs immediately behind the functional one ; in *Nygolaimoidea* the replacement tooth is formed a short distance behind the functional one, whereas in *Dorylaimoidea* this situation only occurs in the first stage juveniles. Indeed, in the other juvenile stages the replacement odontostyle — although formed at the same place as in first stage juveniles, i.e. within the region of the odontophore — is shifted far posteriad.

The oesophagus of *Enoplidae* as well as this of the most primitive *Dorylaimida* is cylindrical ; in both groups its lining is provided with cuticular thickenings for muscle attachment. In *Dorylaimida* none of the oesophageal gland outlets lies anterior to the nerve ring and the dorsal gland outlet is the most anterior one ; the nuclei are normally not concentrated at the base of the oesophagus. In *Ironidae* three oesophageal glands open into the oesophagostome and the opening of the dorsal gland is preceeded by those of the ventrosublateral ones ; the nuclei are concentrated at the base of the oesophagus.

The excretory system of *Ironidae* consists of a longnecked single cell leading to a medioventral pore situated between the first and second circlet of cephalic sense organs ; the cell body occurs near the base of the oesophagus. In *Dorylaimida* the excretory system seems to be degenerate or at least obscure. In those forms for which the system has been reported (some *Mononchida*, *Longidorus*) it consists of two cells whose ducts join before opening through a pore that usually is situated just behind the nerve ring. The structure of the reproductive systems is variable from rather simple to very complicated especially in *Ironidae*, but leaving apart

the secondary complications, the male as well as the female reproductive system of both groups resemble each other in gross morphology. The greatest variation is found in the uterus and although this may be useful to differentiate between the lower taxa, it is not reliable to trace evolutionary lines between higher ones. Until more is known about the cellular anatomy of the systems in both groups comparisons are difficult.

DISCUSSION

A critical appraisal of the similarities between *Ironidae* and *Dorylaimida* leads to the conclusion that they more likely are the result of parallel evolution rather than of close relationship.

The mechanism by which teeth, tooth-like structures or spears are protruded by the action of protractor muscles upon a rigid, sclerotized tube has originated independently in several groups of nematodes. The elongation of the anterior feeding apparatus is apparently advantageous for the functioning of such a system. An elongation has been achieved in all *Ironidae* and concerns the odontophore region, but has only been fully achieved in the more specialised *Dorylaimida* where it also concerns the tooth and the region around it. The elongation apparently was not present in the ancestral form of the *Dorylaimida* and originated within the group, probably in two steps ; it was accompanied by a reduction of the teeth to one. The protractor system in *Ironidae* is clearly of oesophageal origin, that of *Dorylaimida* may be of somatic origin or derived from the sheath that surround the oesophagus. Tooth formation and especially storage of a replacement tooth at some distance behind a functional one is correlated with tooth-size, thickness of the oesophagostomal wall and with the functioning of the anterior feeding apparatus. The phenomenon occurs also in other groups (cf. *Chromadorida*), though less pronounced. In any case it is evident that the condition in which the replacement tooth is stored at some distance behind the functional one has been achieved independently in *Ironidae* and *Dorylaimida*. Indeed, the most primitive *Dorylaimida* have the replacement tooth inside or immediately behind the functional one.

Cuticular thickenings of the oesophageal lining for muscle attachment are rather rare outside *Ironidae* and *Dorylaimida*, they are nevertheless occasionally found in other forms (e.g. *Eurystomina* and *Thoracostoma*, cf. CHITWOOD & CHITWOOD, 1950).

An important difference seems the position of the nuclei and outlets of the oesophageal glands. Since all *Dorylaimida* are comparable in having the outlets and nuclei behind the nerve ring this character was probably present in the ancestral form. On the other hand it should be stressed that this difference may not be overemphasized. Indeed, no other group has developed this situation and hence it can be considered as something typical for *Dorylaimida* (a synapomorphy). Little information is available about the excretory system of *Dorylaimida* except that it usually is considered to be reduced. If the systems so far described represent the typical situation, it is basically different from that of *Ironidae*.

So, while a number of differences can be attributed to special adaptions within each group, some of them seem to be fundamental. In the past the *Ironidae* too often have been compared with the more specialised *Dorylaimina*, while the more primitive *Mononchina* and *Bathyodontina* were overlooked. Therefore it seems that at present sufficient knowledge is lacking to say that the *Dorylaimida* originated from forms near the *Ironidae*.

Fig. 1

Possible evolution of Ironidae and Dorylaimida from Enoplida ancestor.

P = plesiomorph A = apomorph

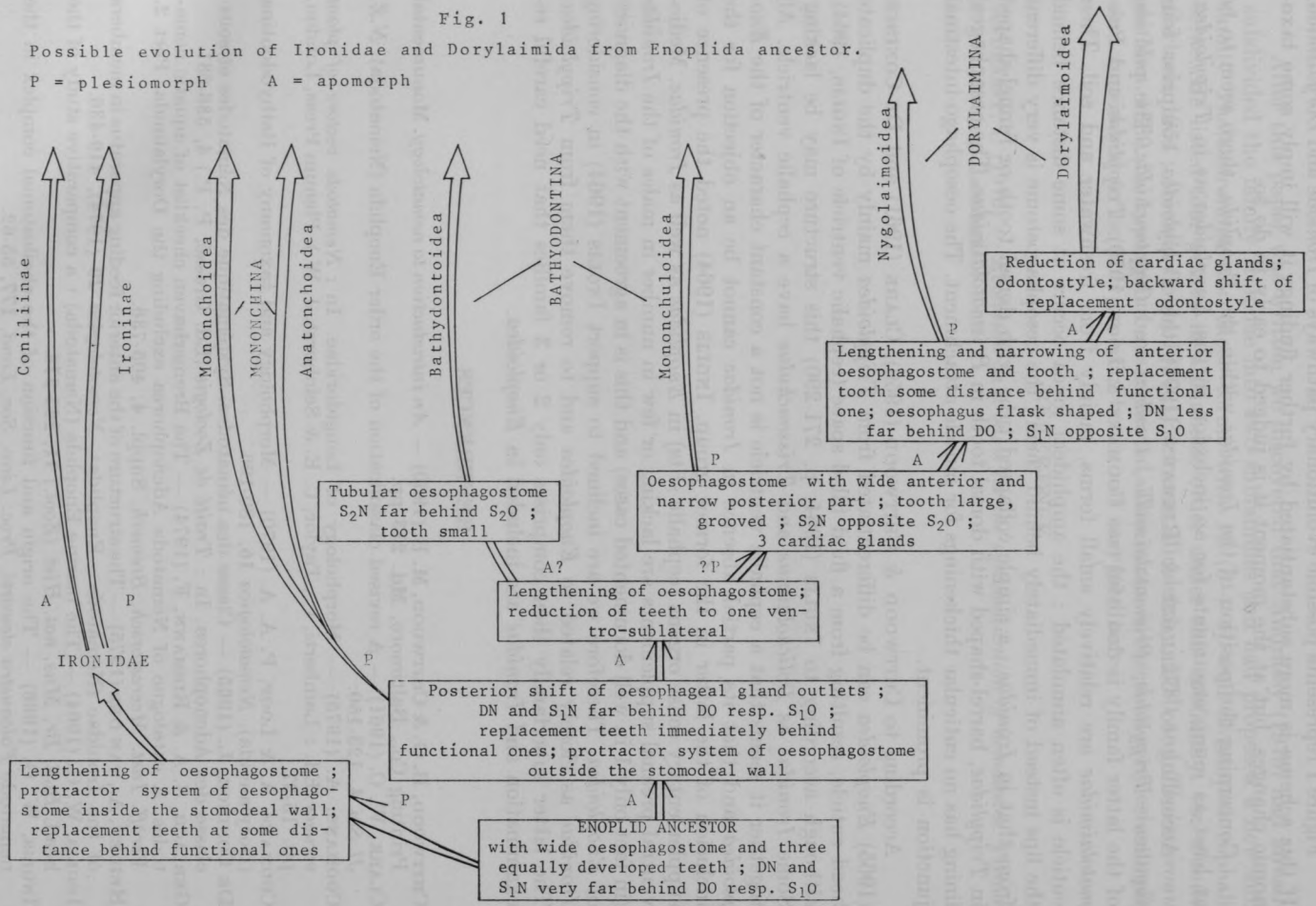

Figure 1 represents possible evolutionary pathways of *Ironidae* and *Dorylaimida*. If this scheme is more substantiated by further findings it will imply some taxonomic changes, but at the moment it is judged to early to do so.

Concerning the position of the *Ironidae* within the *Enoplida*, there seem to be at least as many arguments for an inclusion in the *Enoploidea* as in *Tripyloidea*.

According to GERLACH & RIEMANN (1974) the *Tripyloidea* comprise four families : *Tripylidae*, *Prismatolaimidae*, *Ironidae* and *Cryptonchidae*. The position of the latter family is doubtful (see COOMANS & LOOF, 1970). *Tripylidae* and *Prismatolaimidae* are relatively small forms, mainly from freshwater and soil. Their cuticle is often annulated ; the amphideal fovea occurs at some distance behind the lips instead of immediately behind them ; the oesophagostome is very different from that in *Ironidae* : a simple collapsed tube with dorsal tooth or funnel-shaped in *Tripylidae*, barrel-shaped with dorsal tooth in *Prismatolaimidae*. The oesophageal lining has no cuticular thickenings for muscle attachment. The oesophago-intestinal junction is prominent.

According to CHITWOOD & CHITWOOD (1950), CLARK (1961) and DE CONINCK (1965) *Enoploidea* can be differentiated from *Tripyloidea* mainly by the duplicate head cuticle, resulting from a fluid filled space (cephalic ventricle of INGLIS, 1964), although according to INGLIS (1964, p. 271-290) this structure may be lacking. Some *Ironidae* as *Dolicholaimus* and *Trissonchulus* have a cephalic ventricle. All together it seems that a cephalic ventricle is not a constant character of the *Enoploidea* and that its partial absence in *Ironidae* cannot be an objection for the inclusion of the latter in the former group. INGLIS (1964) noted the presence of supplementary sense organs (cephalic slits) in *Enoplidae* as well as *Ironidae*. Medioventral preanal supplements are lacking or few in number in males of the *Ironidae* (in fact only 1 in well documented cases) and this is in agreement with the diagnosis of *Enoploidea*. Therefore we are inclined to support INGLIS (1964) in considering *Ironidae* as closely related to *Enoploidea* and to remove them from *Tripyloidea*. The latter superfamily then comprises only 2 or 3 families that need careful reexamination and *Ironidae* are included in *Enoploidea*.

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ADDENDUM

After this paper was written we discovered that Andrássy (1976) had already subdivided the family Ironidae into two subfamilies and had proposed a new subfamily Thalassironinae for those forms with 10 (6 + 4) well developed cephalic setae. He listed four genera in alphabetic order under this subfamily, viz. *Conilia* Gerlach, 1954 ; *Ironella* Cobb, 1920 ; *Parironus* Micoletzky, 1930 and *Thalassironus* de Man, 1889. No type genus was indicated. This taxon is based on synplesiomorphy and considered to be polyphyletic, hence not accepted here.

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